NEW LATE PALAEOZOIC HYOLITHA (MOLLUSCA) FROM OKLAHOMA AND TEXAS, AND THEIR PALAEOENVIRONMENTAL SIGNIFICANCE

by JOHN M. MALINKEY, ROYAL H. MAPES *and* THOMAS W. BROADHEAD

ABSTRACT. Recovery of over 900 hyoliths from fourteen localities in Oklahoma and Texas greatly increases the number of late Palaeozoic hyolith occurrences in North America; they include *Lirotheca wilsoni* Malinky and Mapes, 1983 and *Darwinites grafordensis* gen. et sp. nov. Many of the hyoliths lack opercula and taxonomically important features of the aperture, or they are crushed; these specimens are indeterminate. In Oklahoma the hyoliths are restricted to the dark grey to black, non-fissile, phosphatic shale members (= 'core' shales) of Pennsylvanian cyclothems. These shales are thought to be the most offshore facies of the cyclothem. The occurrence of hyoliths in dark grey, locally phosphatic, shale members of cyclothems farther south in Texas further supports the assignment of these shales to offshore, slightly oxygen-poor marine environments rather than to shoreline lagoons.

LATE Palaeozoic hyoliths are little known because of their rare occurrence and generally poor preservation. Hyoliths range from early Cambrian to late Permian, but are only abundant in the Lower Palaeozoic. Bulk sampling of shales in Oklahoma and Texas to recover bactritoid cephalopods (Mapes 1979) has demonstrated that hyolith abundance and diversity are greater in the late Palaeozoic than was previously believed.

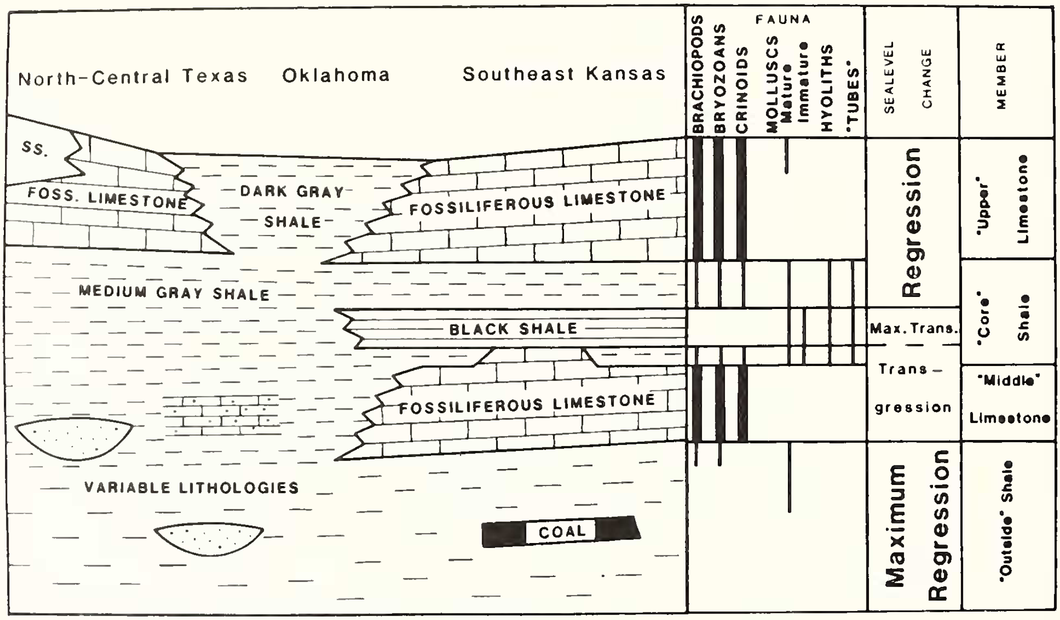
The first record of a Pennsylvanian hyolith is *Hyolithes carbonaria* Walcott, 1884, probably from the Ely Limestone in eastern Nevada. Walcott termed the unit from which he recovered his specimen the 'Lower Carboniferous limestone', although subsequent investigations have demonstrated that unit to be early Pennsylvanian rather than late Mississippian in age (Larson and Langenheim 1979). No other Pennsylvanian specimens were known (Yochelson and Saunders 1967) until *Lirotheca wilsoni* Malinky and Mapes, 1983 was discovered in the Eudora Shale Member of the Stanton Formation in south-eastern Kansas and in the Wolf Mountain Shale Member of the Graford Formation in north-central Texas. The facies in which that species was discovered represents an offshore, oxygen-poor, though otherwise normal marine environment at the Kansas locality (Heckel 1975) and probably at the Texas locality as well (Malinky and Boardman 1983, 1984). *L. wilsoni* was the first hyolith to be recovered from an oxygen-stressed environment in the late Palaeozoic, and the first North American hyolith to be assigned to a genus other than *Hyolithes* Eichwald, 1840. Now over 900 additional specimens have been recovered from localities in Oklahoma and Texas. These specimens enhance our knowledge of the palaeoecology and palaeoenvironmental preferences of late Palaeozoic hyoliths, and help to clarify the concept of *Hyolithes* Eichwald, 1840. Our purpose is to document these occurrences and briefly discuss their palaeoenvironmental significance.

PALAEOENVIRONMENTAL SIGNIFICANCE

Pennsylvanian strata in the northern Midcontinent are dominated by transgressive–regressive lithic sequences, or cyclothems. The furthest offshore unit of each cyclothem usually consists of a fissile black phosphatic shale facies at the base and a non-fissile grey shale facies at the top (text-fig. 1). These facies constitute the 'core' shale (Heckel and Baesemann 1975), so called because it usually

[Palaeontology, Vol. 29, Part 2, 1986, pp. 303–312.]

occupies a central position between an underlying transgressive limestone and an overlying regressive limestone. The black facies is thought to represent an anoxic, offshore, marine environment, deposited below a layer of anoxic water at maximum transgression; the grey shale is interpreted as a dysaerobic offshore facies, emplaced with the partial return of bottom oxygen at the start of regression (Heckel 1977). The lithic character and stratigraphic position of northern Midcontinent 'core' shales provides for their easy recognition; in the southern Midcontinent, however, and particularly in Oklahoma, the distinctive lithic character of the 'core' shales is lost at some localities because the black fissile facies is absent. Additionally, these southern Midcontinent cyclothems are usually dominated by shale which further obscures their cyclicity. The identification of 'core' shales in the southern Midcontinent is therefore made more difficult because of lithic similarities between 'core' shales and the nearshore shales, and because of the absence of limestones. Such shale-dominated cyclothems in this region define the terrigenous-detrital facies belt (Heckel 1968).



TEXT-FIG. 1. Diagram showing distribution of Hyolitha and other commonly occurring macroinvertebrates within Midcontinent Pennsylvanian cyclothems. Relative thickness of vertical lines indicates relative abundance of taxa; thick lines indicate common taxa; thin lines indicate scarce taxa. 'Tubes' refer to problematic organisms of uncertain affinities now under study. Lithologic symbols standard. Cyclothem modified after Heckel (1977).

The palaeontological character of northern Midcontinent 'core' shales is distinctive; the abundance and diversity of conodonts attains a maximum in the black 'core' shale, and several conodont taxa are restricted to that facies (Heckel and Baesemann 1975). In contrast, the distribution of conodonts in some 'core' shales from the terrigenous-detrital facies belt may be irregular and does not follow the patterns seen elsewhere. The 'core' shale interval in these cyclothems was recognized by Boardman *et al.* (1984), using the distribution of macrofaunal assemblages throughout the cyclothem. They amplified and applied the community succession model of Calver (1968), which was derived from faunal distribution in Westphalian cyclothems of Great Britain, to cyclothems in the terrigenous-detrital facies belt. They determined that the *Caneyella*, *Dunbarella*-ammonoid-radiolarian community, which usually occurs in a black, phosphatic shale, occupied the most offshore position, whereas the *Trepospira*, *Sinuitina*-ammonoid-*Anthraconeilo* community, in medium to dark grey shales, occurs in facies marking the start of regression. This latter community has been divided into two, including the *Sinuitina*-juvenile ammonoid-*Anthraconeilo* subcommunity which includes rare corals, trilobites, echinoderms (including blastoids), and sponges; molluscs are common and include gastropods, bivalves, cephalopods, scaphopods, rostroconchs, and polyplacophorans; faunal diversity is high, but the abundance of organisms varies among localities.

The majority of hyoliths collected to date from localities in the terrigenous-detrital facies belt were discovered within dark grey 'core' shales containing the *Sinuitina*-juvenile ammonoid-*Anthraconeilo* subcommunity (text-fig. 1), although the relative abundance of hyoliths in that community is highly variable among localities. Hyolith occurrences in the Smithwick Formation (Atokan) and the Deese Group (Desmoinesian) have not been investigated in the same detail as those from other Midcontinent localities. These two units apparently represent a wide range of environments (Fay *et al.* 1979; Kier *et al.* 1979), although cephalopods, trilobites, blastoids, and other fauna at the same position as the hyoliths suggest that the hyolith-bearing units represent offshore marine environments.

The apparent restriction of Midcontinent Pennsylvanian hyoliths to known 'core' shales in the terrigenous-detrital facies belt in Oklahoma probably reflects a genuine preference for that environment. Numerous early and more recent palaeontological studies of the limestones and other near-shore units in cyclothems (e.g. Mudge and Yochelson 1962; Moore 1964), and recent petrologic and petrographic studies of the limestones (see Heckel 1984, bibliography) have failed to locate hyoliths. Thus, the occurrence of hyoliths only in 'core' shale members of Midcontinent Pennsylvanian cyclothems provides an additional tool for the recognition of such 'core' shales in areas where other evidence is inconclusive or ambiguous.

The cyclic nature of Pennsylvanian strata in north-central Texas has long been recognized, although the furthest offshore unit has been in dispute. Diversely fossiliferous shales above the basal fluvial/deltaic package in these cyclothems have formerly been interpreted as lagoonal in origin (Erxleben 1975), with the overlying limestone regarded as the most offshore facies. Malinky and Boardman (1983, 1984) suggested that the fossiliferous shale is a 'core' shale, depositionally similar to those from northern Midcontinent localities. This interpretation is base upon high faunal diversity, the presence of phosphate nodules at many localities, and diagenetic patterns in the limestone members of these cyclothems. Hyoliths have been recovered only from the diversely fossiliferous shale members of Texas cyclothems, such as the Wolf Mountain Shale (Graford Formation; Missourian), the Finis Shale, Bluff Creek Shale, and Wayland Shale (all Graham Formation; Virgilian). Their occurrence in the shale facies suggests that such units are 'core' shales and supports the assignment of these shales to offshore marine environments rather than to marginal marine lagoons.

SYSTEMATIC PALAEONTOLOGY

Introductory comments. Outside Eastern Europe and the Soviet Union the taxonomy of the Hyolitha has long been neglected, and remains particularly underdeveloped in North America. The generic name *Hyolithes* Eichwald, 1840 has been extensively used for many North American hyolith species; at one time it encompassed over 360 species (Sinclair 1946). This broad generic concept is the result of a vague and generalized original description of *Hyolithes* by Eichwald (1840, p. 97) in which only the sub-triangular transverse outline of the shell and the presence of apical septae were noted. Much of the original description consisted of discussion of possible affinities, a matter still of argument. Consequently, a variety of organisms possessing shells with generally sub-triangular transverse sections came to be included in *Hyolithes*. All species now encompassed by that genus warrant re-examination.

Syssoiev (1958, 1959) emended *Hyolithes* but still retained a variety of transverse shapes within the genus. We prefer a generic concept more closely conforming to Eichwald's original specimens as illustrated by Fisher (1962, p.W123, fig. 67.1*a*–*d*). We consider *Hyolithes* to have a broad, depressed dorsum, grading into a pronounced longitudinal sulcus at each edge of the dorsum, and rounded lateral margins. The venter is slightly inflated and the ligula is low and ventrally curved. The dorsal apertural margin has a flare and the transverse section is sub-triangular. The apical end of the shell curves dorsally. The operculum is unknown.

The standards of quality for type specimens of *Hyolithes* species have changed. Now only specimens retaining well-preserved apertural detail should be used as types. The apertural features, as well as a number of other characters of the conch and operculum, have been used for generic and specific level taxonomy (Marek 1966*a*) although we judge that a well-preserved conch lacking an operculum, or even the internal mould of the conch, can be confidently identified to genus and species in some taxa.

Repository. All specimens are housed in the National Museum of Natural History, Washington, DC.

Phylum MOLLUSCA
Class HYOLITHA Marek, 1963
Order HYOLITHIDA Matthew, 1899
Family HYOLITHIDAE Nicholson *fide* Fisher, 1962
Genus DARWINITES gen. nov.

Type species. *Darwinites grafordensis* gen. et sp. nov.

Diagnosis. Hyolith having a small ligula on the ventral apertural margin, a low dorsal ridge with flattened flanks, and a depressed sub-triangular transverse section; the aperture is expanded noticeably, and the mould tapers rapidly to a pointed apex.

Discussion. The absence of longitudinal sulci and an apertural flare on the dorsum of *Darwinites* clearly distinguish it from *Hyolithes*. Furthermore, *Darwinites* possesses a dorsum with a narrowly rounded median keel, whereas the dorsum on *Hyolithes* is rounded. The low ventral shelf, narrowly rounded dorsal ridge, and conical shape of *Darwinites* separate it from *Lirotheca* Malinky and Mapes, 1983 (from the Pennsylvanian of Kansas). Furthermore, the dorsal ridge on *Lirotheca* is inflated rather than depressed and the ventral ligula is larger. These features support generic status for *Darwinites*.

Etymology. This genus is named for Darwin R. Boardman in recognition of his work in field and laboratory studies of Midcontinent stratigraphy and palaeontology.

Darwinites grafordensis gen. et sp. nov.

Text-fig. 2A–C

Diagnosis. See genus.

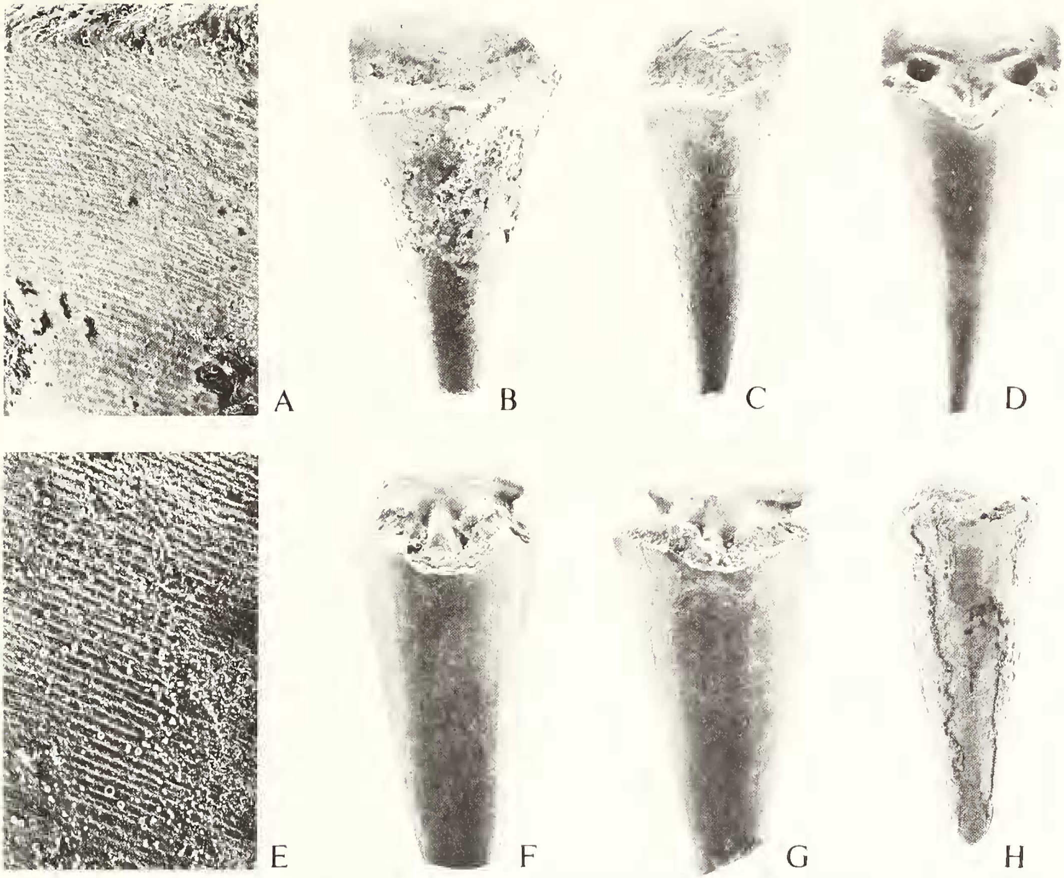
Material. Three specimens: holotype, USNM 390488, loc. V-2, Virgilian; paratype, USNM 390487, loc. M-3, Missourian; and paratype, USNM 390489, loc. V-3, Virgilian. See Appendix for locality details.

Description. The dorsum possesses a low median dorsal ridge, with a narrowly rounded crest and flattened flanks adjacent to it. The lateral margins are broadly rounded and the venter is flat with a small ligula along the apertural margin. The transverse shape is depressed, and the mould tapers rapidly toward the apex. The apex curves slightly toward the dorsum.

Closely spaced transverse lirae occur on the internal mould of the dorsum (text-fig. 2A), and a faint sulcus is present along each edge of the venter near the apertural end. The operculum has a single set of clavicules (monoclaviculate). The conical shield is large and flattened, whereas the cardinal shield is smaller and indistinct. Other details of the mould and the shell are unknown.

The three specimens occur as limonitized internal moulds and only the holotype is well preserved. The holotype is 2·5 mm long, with an apertural width (W) of 2·5 mm and apertural height (H) of 1·7 mm. The paratypes are comparable in size.

Discussion. *Darwinites* is monospecific. *D. grafordensis* is the second hyolith species to be discovered in the Midcontinent Pennsylvanian of North America, and only the second North American hyolith



TEXT-FIG. 2. SEM photomicrographs of Midcontinent Pennsylvanian Hyolitha. All specimens are internal moulds. A–C, *Darwinites grafordensis* gen. et sp. nov. A, lirae on left flank of dorsum, holotype, USNM 390488, Virgilian, loc. V-2, ×240; B, dorsum, holotype, ×20; C, dorsum, paratype, USNM 390487, Missourian, loc. M-3, ×20. D, *Lirotheca wilsoni* Malinky and Mapes, 1983; dorsum showing prominent moulds of clavicles on operculum, hypotype, USNM 390490, Virgilian, loc. V-2 ×10. E–H, Hyolitha *incertae sedis*. E, lirae on left flank of dorsum, USNM 390468, Desmoinesian, loc. D-1, ×240; F, dorsal view showing fragmentary monoclaviculate operculum, USNM 390466, Desmoinesian, loc. D-1, ×8·2; G, dorsal view showing fragmentary operculum, USNM 390495, Virgilian, loc. V-3, ×5·4; H, venter, USNM 390485, ×5·0.

taxon assigned to a genus other than *Hyolithes*. Similarly preserved species belonging to closely related genera include *L. wilsoni* Malinky and Mapes, 1983. Differences between those genera have been noted above.

Etymology. The species is named for the Graford Shale, in which hyoliths were first discovered in Texas.

Genus LIROTHECA Malinky and Mapes, 1983

Types species. *Lirotheca wilsoni* Malinky and Mapes, 1983, p. 348.

Diagnosis. Hyoliths having a narrowly rounded dorsum with a prominent flare along the dorsal apertural rim and a ventral ligula; the dorsum has a narrowly rounded median keel; the transverse section is inflated and sub-triangular.

Discussion. Differences between this genus and *Hyolithes* Eichwald, 1840 were noted by Malinky and Mapes (1983), while differences between it and *Darwinites* were discussed above. The occurrence of *Lirotheca* at new localities in Oklahoma and Texas extends its geographic range from south-eastern Kansas, and its discovery in Virgilian strata extends its stratigraphic range from Missourian only into the Desmoinesian and Virgilian.

Lirotheca wilsoni Malinky and Mapes, 1983

Text-fig. 2D

1983 *Lirotheca wilsoni* Malinky and Mapes, p. 348, fig. 1A–C, F, G.

Diagnosis. See genus.

Material. Four specimens: hypotypes, USNM 390490 and 390491, loc. V-2, Virgilian; USNM 390492, loc. D-1, Desmoinesian; and USNM 390493, loc. V-3, Virgilian. See Appendix for locality details.

Description. The dorsum is inflated and possesses a narrowly rounded median keel with inflated flanks adjacent to it. The lateral margins are rounded, and shallow indentations occur on the apertural rim along the lateral margins. A shallow sinus also occurs along the aperture where the dorsal keel and apertural rim intersect, and the entire apertural rim is flared. The venter is flat, and the ventral ligula is strongly curved toward the venter. The apex curves slightly toward the dorsum.

Faint transverse lirae cover much of the dorsum. The lirae are straight across the flanks of the dorsal ridge but curve on the ridge crest to create a shallow sinus. Transverse lirae also cover much of the venter. A sulcus is present along each margin of the venter; each extends from the shelf about three-quarters the length of the mould toward the apex.

The operculum is monoclaviculate with well-developed clavicles near the dorsal edge. The conical shield on the ventral side is flat whereas the dorsal cardinal shield and furrows are inconspicuous. No lirae occur on the operculum.

Discussion. The recovery of these larger, well-preserved specimens of *L. wilsoni* affords the opportunity to supplement the description of the holotype and paratypes, especially concerning details of the operculum. On the holotype the clavicles are covered with sediment, whereas on these specimens the clavicles are well exposed, so that their monoclaviculate nature is certain. The holotype from the Eudora Shale in Kansas is smaller than the specimens described above, and may represent a juvenile.

Class HYOLITHA *incertae sedis*

Text-fig. 2E–H; Table 1

Material. More than 900 specimens, with a distribution among localities shown in Table 1. See Appendix for locality details.

Description. The dorsum on specimens included under this heading varies from depressed to inflated, and the keel on the dorsum varies from angular to narrowly rounded. The lateral margins on most are also narrowly rounded, and the venter ranges from flat to slightly inflated. The transverse section varies from inflated to depressed sub-triangular. All specimens are elongate, reflecting a low angle of apical expansion.

The apex varies from straight on most specimens to curved, either dorsally or ventrally, or to the left or right when viewed from the dorsum. A few specimens have fragmentary monoclaviculate opercula; otherwise no apertural detail is known.

Most specimens are preserved as limonitized internal moulds. The moulds are generally smooth, although on a few specimens they show faint, closely spaced, transverse lirae near the apertural end. Some specimens, particularly those from the Deese Group, retain shells, but they are crushed, partially dissolved, and preserve little detail. All other features of these specimens are unknown.

Discussion. Specimens included under this heading are regarded as *incertae sedis* below the class level because they lack the apertural features necessary to confidently assign them at lower taxonomic levels. Three orders are currently included in the class Hyolitha: the Hyolithida, Orthothecida, and Toxeumorphida (Peel and Yochelson 1984). The Hyolithida are distinctive because of the ligula along the ventral apertural rim; their opercula are subdivided into cardinal and conical shields separated by furrows, and the interior of the opercula possesses one or more pairs of processes termed clavicles (Marek 1966*a*, p. 71, fig. 10A–C); transverse sections are sub-triangular. The Orthothecida lack the ventral ligula, and their opercula have neither shields nor interior clavicles (Marek 1966*b*, p. 91, figs. A, B); transverse sections on some are kidney-shaped whereas on others they are sub-triangular like those of hyolithids (Marek 1966*a*, p. 59, fig. 3). The Toxeumorphida are poorly known, although available specimens suggest strongly that their transverse shapes are circular. All the current specimens have sub-triangular transverse sections, so that the Toxeumorphida are probably not represented.

TABLE 1. Distribution of hyoliths listed under Hyolitha *incertae sedis* in southern Midcontinent 'core' shales. Details of localities are given in the Appendix. Sample weights are approximate. All specimens have been deposited at the National Museum of Natural History (USNM).

Locality	*Sample weight (kgm)*	*Number of specimens*	*Number*
A-1	2000	19	390463
A-2	270	7	390464
D-1	136	571	390465–390469, 390481, 390483, 390484, 390494
D-2	22·7	1	390470
D-3	109	5	390471
D-4	680	3	390472
D-5	109	33	390473
M-1	0·5	1	390474
M-2	0·5	2	390475
M-3	680	47	390476, 390495, 390496
V-1	45	1	390477
V-2	432	195	390478, 390482
V-3	432	134	390479, 390485, 390486
V-4	108	4	390480

Except for the few specimens retaining fragmentary opercula (text-fig. 2F, G), no Pennsylvanian specimens can be confidently placed in either the Hyolithida or Orthothecida. The specimens with opercula are undoubtedly hyolithids because the remains of clavicles are clearly evident on the opercula, despite poor preservation otherwise. Among the other specimens the lack of well-preserved apertural characteristics preclude distinction between the Hyolithida and Orthothecida. By themselves, transverse outline, lirae, or other features of the moulds cannot be used to diagnose or recognize hyolith taxa at any level (Marek 1966*a*). Better preserved specimens from Oklahoma and Texas may demonstrate that several taxa are present in the Midcontinent Pennsylvanian .

Acknowledgements. Partial support for this study was provided by the Smithsonian Institution in the form of a Postdoctoral Fellowship to J. M. M. Thanks are due to the Ohio University Research Committee and to the donors of the Petroleum Research Fund, administered by the American Chemical Society, for partial support to R. H. M. (PRF No. 15821-AC2). We thank E. L. Yochelson (U.S. Geological Survey) and R. E. Grant (National Museum of Natural History) for their comments on the manuscript. Heidi Wolff assisted with the SEM.

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JOHN M. MALINKY
Department of Paleobiology
National Museum of Natural History
Washington, DC 20560, USA

ROYAL H. MAPES
Department of Geology
Ohio University
Athens, Ohio 45701, USA

THOMAS W. BROADHEAD
Department of Geological Sciences
University of Tennessee
Knoxville, Tennessee 37996, USA

Typescript received 6 March 1985
Revised typescript received 13 September 1985

APPENDIX

List of localities

ATOKAN

A-1: Smithwick Formation. Shale exposed 5·6 km east and 1·4 km south of US Highway 190 and county road FM 1121 junction, near Rochelle, McCulloch Co., Texas (Speck Mountain 7·5′ quad.; Mapes and Furnish 1981).

A-2: Atoka Formation. Shale exposed on the north bank of Delaware Creek approximately 100 m east of state highway 48, approximately 2·4 km north of Wapanucka, Johnston C., Oklahoma (NW1/4 SW1/4 SW1/4, sec. 1, T2S, R8E, Wapanucka 7·5′ quad.).

DESMOINESIAN

D-1:Deese Group. Limited shale exposure in cutbank of unnamed stream on the Daube Ranch, near Mannsville, Johnston Co., Oklahoma (SW1/4 SW1/4 SE1/4, sec. 31, T3S, R4E, Mannsville 7·5′ quad; loc. P-10 of Mapes 1979).

D-2: Atwood Shale (Lower Wewoka 2). Shale exposed on north side of state highway 12, 3·8 km south-west of the junction of state highways 12 and 48 in Allen, Pontotoc Co., Oklahoma (SW1/4 SE1/4, sec. 13, T5N, R8E, Lake Holdenville 7·5′ quad.).

D-3: Wewoka Shale. Shale exposed in the east bank of unnamed stream at the shoreline of Lake Okmulgee in Okmulgee State Recreation Area, 9·6 km west of Okmulgee, Okmulgee Co., Oklahoma (NE1/4 SE1/4 SW1/4, sec. 18, T13N, R12E, Lake Okmulgee 7·5′ quad.).

D-4: Wewoka Shale. Shale exposed 3·2 km east and 3·2 km south of Homer, Pontotoc Co., Oklahoma. Shale crops out 120 m east of north–south road in a gully (S1/2 NW1/4 SW1/4, sec. 4, T3N, R7E, Francis 7·5′ quad.; loc. P-8 of Mapes 1979).

D-5: lake Neosho Shale Member of Altamont Formation. Shale not in place; exposed in a now overgrown vacant lot adjacent to and parallel with US Highway 51, 0·2 km south of 129th St. exit, Broken Arrow, Tulsa Co., Oklahoma (NE1/4 NE1/4, sec. 32, T19N, R14E, Broken Arrow 7·5′ quad.).

MISSOURIAN

M-1: unnamed shale (probably equivalent to Exline). Shale exposed in stream bank south-west of Mound Valley, Labette Co., Kansas (centre line west, SE1/4 NW1/4, sec. 25, T6N, R7E, Mound Valley 7·5′ quad.).

M-2: Tackett Shale (probably equivalent to Exline). Shale exposed in a series of gullies 2·4 km north of Sasakwa, Seminole Co., Oklahoma (centre line west, SE1/4 NW1/4, sec. 25, T6N, R7E, Sasakwa 7·5′ quad.).

M-3: Wolf Mountain Shale Member of Graford Formation. Shale exposed in a construction site for a housing project on west side of Lake Bridgeport; exposure is 0·8 km west and 0·8 km south of the junction of US Highway 380 and the Lake Bridgeport bridge, Wise Co., Texas (Wizard Wells 7·5′ quad.; loc. 3 of Tucker and Mapes 1978; and see Malinky and Mapes 1983).

VIRGILIAN

V-1: Finis Shale Member of Graham Formation. Shale exposed 0·8 km north-east of oil storage tanks on Curtis Ranch, 1·9 km east of US Highway 281, 3·5 km south-east of Jacksboro, Jack Co., Texas (Jacksboro Northeast 7·5′ quad.).

V-2: Bluff Creek Shale Member of Graham Formation. Shale exposed 1·6 km south-east of end of a private road near a pond dam; the road is located 9·6 km north-east of Whon, along the road connecting Whon and Trickham, Coleman Co., Texas (Speck Mountain 7·5′ quad.).

V-3: Bluff Creek Shale. Exposure located near a pond dam 0·69 km east of county road FM 568 and 17·5 km south of Bangs, Brown Co., Texas (Bangs 7·5′ quad.).

V-4: Wayland Shale Member of Graham Formation. Shale exposed on south-west side of hill 0·2 km north of road connecting Whon and Trickham, and 2·6 km east of intersection of that road and the private road leading to locality V-1, Coleman Co., Texas (Speck Mountain 7·5′ quad.).